SONGS AND CALLING BEHAVIOUR OF *FROGGATTOIDES*TYPICUS DISTANT (HEMIPTERA: CICADOIDEA: CICADIDAE), A NOCTURNALLY SINGING CICADA

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Abstract

The nocturnal male singing behaviour and songs of *Froggattoides typicus* Distant are documented, based on observations and sound recordings made at the Southwood National Park in southern Queensland, during early December 2005, in an open net after dusk. Two distinct song components are recognized: (i) a continuous, soft clicking song (calling song) with some accompanying clicks and click phrases, emitted during the earlier part of the evening and believed to be predominantly timbal produced; (ii) sets of multiple ticks produced during the later part of the evening, commonly accompanying wing flicking behaviour and together with sporadically emitted, short, sharp buzz phrases which sound similar to the sudden expulsion of air from a restricted nozzle.

Introduction

Known by its popular name 'eastern bent-winged cicada' (Moulds 1990), Froggattoides typicus Distant is a very distinctive, predominantly pale green, endemic Australian cicada. Moulds (1990) noted that it had never been heard singing, at least during the day. It is, however, frequently captured at light, usually arriving well after sunset, when it commonly appears in significant numbers and often emits a marked clicking noise. As noted by Moulds (1990), hand-held specimens of both sexes produce an audible clicking noise, apparently resulting from a rapid beating together of the distal half of the wings while closed. The production of click sounds in this species may, however, also involve an alternative mechanism as the wings are flicked open, generated when the forewing leaves the wing grooves on the margins of the mesonotum (Ewing 1989; see also Gogala and Trilar 2003).

F. typicus occurs widely throughout southern, southwestern and central Queensland, being noticeably common in forest communities associated with brigalow (Acacia harpophylla) and gidyea (A. cambagei) woodlands. It is very rarely seen during the day, sitting camouflaged in tree foliage. We were initially alerted to the nocturnal behaviour of F. typicus by observations made of insects calling after 2000 h on the highway between Charleville and Cunnamulla, southern Queensland (S. Peck, pers. comm.). Our observations indicate that it is indeed nocturnally active, with song production only after dusk. Such behaviour is unusual within known Australian Cicadidae, which predominantly sing during the day and/or at dusk (see Moulds 1990).

Materials and methods

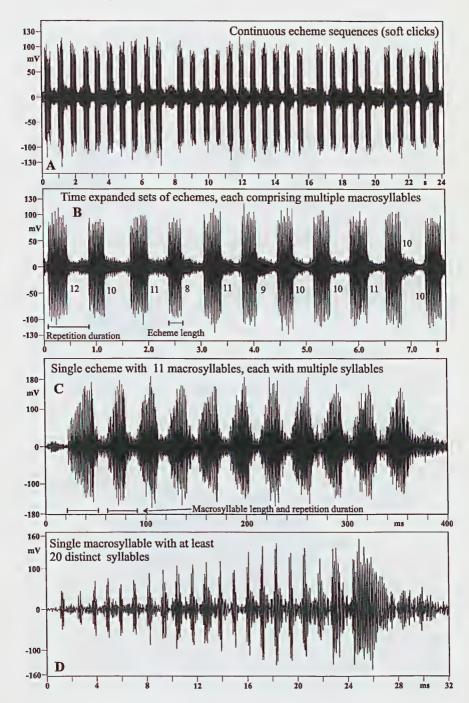
Observations and recordings were collected in brigalow forest in the Southwood National Park (~27°50'S 150°06'E), southern Queensland,

between 5-9 December 2005. Recordings were made with a Sony cassette recorder WM-D6C, with Sennheiser microphone K6/ME66. Song analyses utilised Avisoft SASLab Pro4 software. After capture at light, the insects were placed in a cylindrical net cage (36 cm x 30 cm diameter), containing small fragments of local vegetation, and placed in a canvas tent (3 x 2 x 2 m) with no artificial lighting but with one window uncovered to allow entry of filtered weak moonlight. Some of the insects were kept alive in the net cage during the following day under strongly shaded conditions. Song and timbal terminology follows that used by Ewart (2005). Amplitude spectra were produced using a 556-point Fast Fourier Transform with Hamming window.

Singing behaviour

During and especially after dusk the cicadas became active, constantly moving around the vegetation with frequent wing 'flicking'. This activity continued until or slightly beyond midnight. The nature of 'song' production, however, changed between the earlier and later parts of the evening. During the observation period, sunset and end of civil twilight occurred at approximately 1848 h and 1915 h (Eastern Standard Time) respectively. From approximately 2030-2115 h the cicadas, while still actively walking around the vegetation in the cage, produced a continuous, soft clicking song (Fig. 1), sporadically interspersed with sets of regularly emitted and regularly spaced clicks as well as short, sharp and relatively loud individual clicks (Figs 2A-C), in some cases visibly associated with wing flicking. After approximately 2115 h, the soft clicking song became progressively more subdued and ceased. Instead, the cicadas continued to be active, constantly (but erratically) flicking their wings, which produced very short sets of distinct multiple clicks (Fig. 3A), not exactly the same in structure as those emitted earlier, together with additional and very sporadic short sharp 'buzz' phrases (Fig. 3D); this activity continued to slightly beyond midnight. All song types recorded during this study were produced by male insects only.

Fig. 1. Waveform plots (amplitude versus time) of the early evening calling song of Froggatoides typicus. (A): the continuous echeme sequences, each echeme sounding as a soft click; the low amplitude phrases occurring between some of the echemes are due to the songs of other F. typicus in the background; recording filtered (IIR) to 5.5 kHz. (B): expanded time plot showing the multiple macrosyllables comprising each echeme, the numbers associated with each echeme showing the numbers of macrosyllables present; the definitions of echeme lengths and repetition rates are shown [as also in A]. (C): further time expanded plot of a single echeme showing individual macrosyllables, each comprising multiple syllables. (D): details of individual syllables within the initial macrosyllable shown in Fig. C; also note the long final syllable, possibly indicating syllable coalescence. Records B to D filtered (IIR) to 1 kHz.



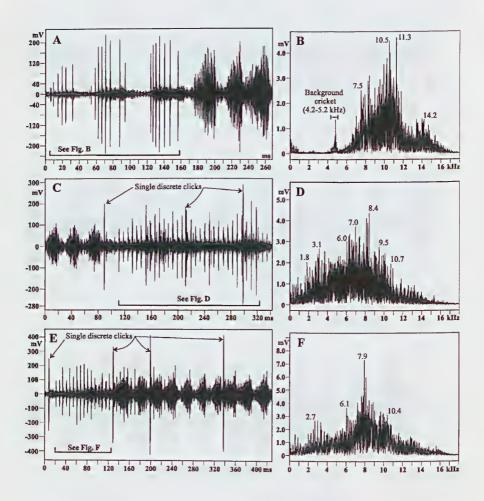


Fig. 2. Waveform plots (A, C, E) and their respective amplitude spectra (B, D, F; amplitude vs frequency) of early evening clicking sounds of *Froggatoides typicus*. (A-B): three groups of single clicks, each group with changing repetition rates, emitted between calling song echeme; individual clicks have broadband frequency spectra with dominant frequencies between 8.4 and 11.0 kHz; amplitude spectrum shown is based on all three groups. (C-F): temporally patterned clicks emitted at beginning and end of a sequence of calling song echemes; individual clicks include both single and double pulses; additional higher amplitude isolated single clicks are shown, which may not have been emitted by the same insect; these clicks are single pulses, with narrowband frequency spectra and dominant frequencies between 6.9 and 7.9 kHz.

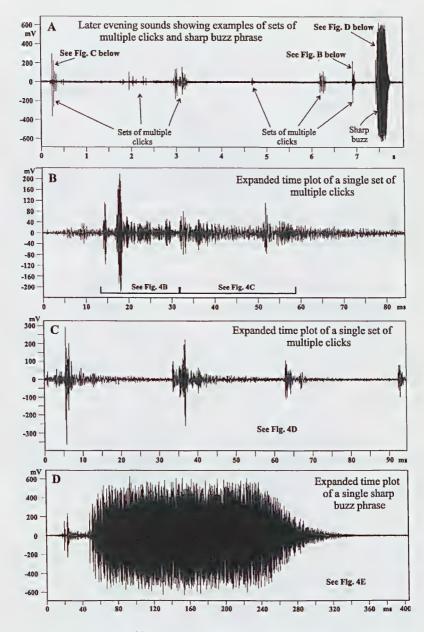


Fig. 3. Waveform plots of later evening clicks and 'buzz' sounds of *F. typicus*. (A): sets of multiple sets of clicks and the short sharp 'buzz' phrase. (B-C): time expanded plots of two sets of clicks shown in Fig. A. (D): expanded time plot of the single sharp 'buzz' phrase shown in Fig. A. Recordings A to D filtered (IIR) to 1 kHz.

Song analyses

(a) Early evening continuous soft clicking song (Fig. 1)

This consisted of continuous echeme sequences, each echeme producing a single audible click. The mean repetition rate was 1.35 s⁻¹ (range 1.2-1.5) and mean echeme length was 325 ms (range 267-378). Each echeme, as seen in expanded time plots (Figs 1B-C), comprised a sequence of macrosyllables, 8-12 in number, with a mean length of 21.7 ms (range 16.4-30.3), the variation reflecting the number of component macrosyllables. Macrosyllable repetition rates varied from 24-37 s⁻¹ (27.9-41.5 ms). The initial macrosyllable in each echeme was the longest. Each macrosyllable was further resolved, at further time expansion (Fig. 1D), into 16-24 discrete syllables. Syllable repetition rates varied from 295-2040 s⁻¹ (mean 910), equivalent to syllable lengths of 0.49-3.4 ms (mean 1.13); these equated closely to the syllable amplitude modulation of 885 s⁻¹. The final two high amplitude syllables within each macrosyllable apparently have coalesced, as illustrated by the macrosyllable shown in Fig. 1D.

The amplitude spectrum (Fig. 4A) of the continuous clicking song component shows the emitted frequency maxima to lie between approximately 7 and 9 kHz, with significant frequency peaks, with reduced magnitudes, extending to 16 kHz. The spectrum is notable for the extensive array of apparent sidebands (listed in Fig. 4A), their complexity attributed to the complexity of the fine scale variability within the macrosyllable and syllable structures. Very detailed time plots and amplitude spectra of the syllables (not shown) indicated that the final high amplitude syllables (as shown in Fig. 1D) are characterised by a rather narrow band of frequency emission centred at 7.2 kHz, the frequencies slightly decreasing during syllable emission and rising markedly either side of the syllable. In contrast, the initial 5 syllables shown in Fig. 1D had frequencies between 9.4 and 10.1 kHz, compared with the low amplitude inter-syllable regions which exhibited higher frequencies between 10.6 and 11 kHz. These demonstrate rapid temporal changes in frequencies during syllable emission, on time scales of <1 ms.

(b) Early evening click phrases and single clicks

Short phrases, less than 300 ms in length and comprised of temporally structured clicks, were observed to be sporadically interspersed within, or between, the echemes of the continuous soft clicking song (Fig. 2). The regularly emitted click phrases (Figs 2C-D) had click repetition rates of 145-146 s⁻¹ and comprised both single and doublet pulses. When emitted as short groups of clicks (each single pulses: Fig. 2A), the click repetition rates decreased during emission. The frequency structures of these structures click phrases are variable (Figs 2B, D, F), ranging from relatively sharply tuned frequency maxima near 8 kHz (Fig. 2F), to more broadband frequency maxima between about 8 and 11.5 kHz (Fig. 2A), to very broadband frequency distributions between 2 and 11 kHz (Fig. 2D).

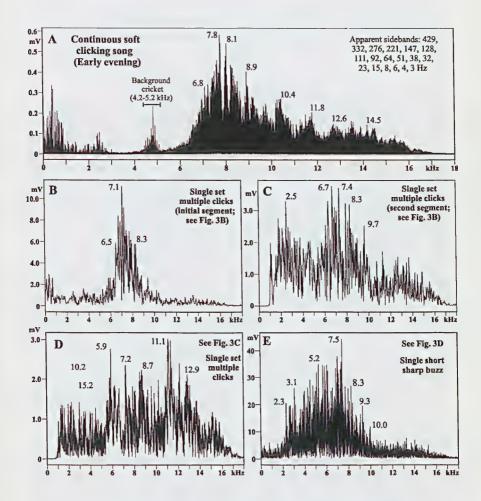


Fig. 4. Amplitude spectra of *Froggatoides typicus* songs. (A): multiple echemes (40 seconds) of the continuous soft calling song shown in Fig. 1A; note the weak background song of an unidentified cricket between 4.2 and 5.1 kHz. (B-C): initial and later segments, respectively, of the set of clicks shown in the expanded time plot in Fig. 3B. (D): set of multiple clicks shown in the expanded time plot in Fig. 3C. (E): The short 'buzz' phrase shown on Fig. 3D. Spectra shown in Figs C and D filtered (IIR) to 1 kHz.

The relatively higher amplitude sharp single clicks (Figs 2C, E) are emitted apparently randomly during the continuous soft clicking song. Expanded time plots (not shown) showed these to be narrowly tuned single pulses with relatively narrow dominant frequency spectra between 6.9 and 7.9 kHz. Those shown in Figs 2C-D may not all emanate from a single insect in the cages.

(c) Later evening sets of multiple clicks (Fig. 3A)

These are here linked to wing 'flicking' behaviour accompanying the constant walking activity. The timing between the sets of clicks was very variable although they were emitted frequently. Individual sets of clicks varied in detailed structure, as seen in expanded time plots (Figs 3B-C). Within a given set, individual clicks ranged from 2 to 12 in number. Their structures also varied, some comprising high amplitude pulses with logarithmically decaying tail, others that were relatively closely spaced and partially coalescing, with extended complex decaying tail (Fig. 3B). The initiation of the high amplitude pulse trains of the clicks were mostly abrupt and were commonly preceded (~5-10 ms interval) by a sharp, low amplitude pulse or pulses. The two sets of amplitude spectra illustrated (Figs 4B-D) exhibit strongly contrasting frequency patterns, particularly in the click sequence shown in Fig. 3B. The initial segment of this sequence had a narrowband frequency structure between 6.5 and 8.5 kHz (Fig. 4B). The following segment of the click sequence (Fig. 4C) exhibited broadband frequency emissions between ≤1 and 10 kHz, extending with reduced amplitude to 15 kHz. The most significant difference between these two spectra was the presence of a strong lower frequency component below 5 kHz in the later segment of the ticking sequence, which we attribute to wing flicking (see below). The amplitude spectrum of the click sequence shown in Fig. 3C exhibits an extremely broad frequency emission extending between ≤ 1 and 16 kHz (Fig. 4D).

(d) Later evening short sharp 'buzz' phrases (Fig. 3D)

These clearly differ from the sets of clicks previously described. Those measured ranged between 0.3 and 0.35 s in length. They are abrupt, relatively loud and emitted only sporadically and irregularly. To the human ear, they have a distinct resemblance to the sudden expulsion of air from a restricted nozzle. As shown by the waveform plots (Fig. 3D), they initiate abruptly, continue briefly at constant amplitude and decay nearly exponentially. A small precursor double pulse is present. The amplitude spectra showed a broad frequency emission range between approximately 2 and 10 kHz, with maxima near 7-7.5 kHz (Fig. 4E). There appeared to be an absence of clearly defined temporal patterning and thus the overall structure was similar to white noise. The small precursor pulse phases exhibited a very narrowly tuned spectrum between 6.7 and 8.1 kHz, quite distinct from that of the main phrase.

Discussion

The early evening continuous soft clicking song is interpreted as a timbalgenerated calling song with a dominant frequency range between ~6.5 and 9 kHz. Although a cursory examination of the timbals suggest that they are poorly developed, this is only because they are effectively 'sandwiched' between the bulbous tergites 1 and 2 (Figs 5B, 6B) and require the removal of much of tergite 2 to be fully visible (Fig. 5A). They are similar in overall form to those of diurnally singing cicadas. The six timbal ribs (long ribs) are very pale green in colour and weakly sclerotised. The four posterior ribs (1 to 4) are fused dorsally to the basal spur and ventrally to each other. Ribs 1 to 3 are continuous across the timbal, whereas rib 4 is discontinuous medially. The two most anterior ribs (5, 6) are short, unfused and appear to represent remnant long ribs. No inter-rib sclerites between ribs 1 to 4 were observed. The dorsal and ventral fusion of ribs 1 to 4 suggest that these may act as a single rib during timbal contractions and relaxation, as suggested in certain diurnal ticking cicadas (Ewart 2005). The male opercula are well developed and also similar in overall structure to those of diurnal cicadas (Fig. 6A). Those in F. typicus are notable for the absence of spikes on the meracantha and the marked curvature and undulations of the surfaces of the opercula, the latter best seen in lateral profile (Fig. 6B).

The various clicking sounds shown above exhibit complex frequency spectra varying between narrowband and very broadband. As described, wing flicking occurs frequently during early and later evening songs. Some clicks were observed to correlate with wing flicks, suggesting that both timbals and wing flicks are used, either singly or in combination, as part of song production. An additional factor is the differential role of sound radiation structures (timbals, tympana and abdomen) in modulating the frequency signatures of the emitted sounds (Fonseca and Popov 1994).

We suggest that the earlier evening songs are predominantly timbal produced, including the patterned and separate click components, which we further correlate with dominant spectral frequencies between approximately 6-11 kHz (e.g. Figs 2B, 2F; 4A, 4B). Nevertheless, many clicks have dominant frequencies which include a significant component at <6 kHz and in some clearly extend to >11 kHz (e.g. Figs 4C-D). We interpret these clicks and their spectral frequencies to have originated predominantly through wing flicking. The later evening clicks are mainly, but not entirely, of these types. Nevertheless, amplitude spectra of some clicks, including early and later evening types, showed frequencies which suggest the presence of both timbal and wing clicking components (e.g. Figs 2D, 4B-C), pointing to combined timbal and wing flicking in sound production. The short sharp 'buzz' phrases are enigmatic in their origin. Both their structure, as seen in the waveform plots, and their frequency spectra distinguish them from the other sounds produced by F. typicus, implying a different production mechanism. As noted

above, the sound resembles a sharp expulsion of air. The frequency spectrum of the precursor pulses, however, suggests that these may initiate via a timbal origin.

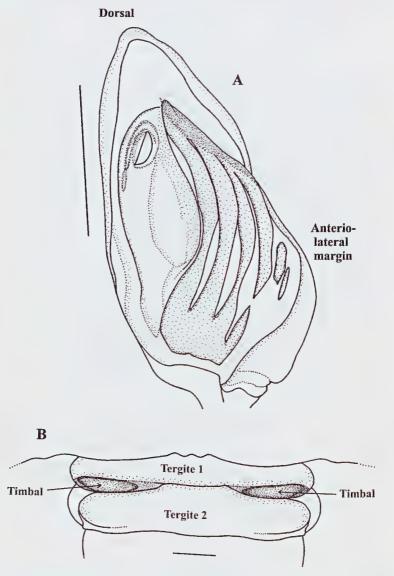


Fig. 5. Froggattoides typicus. (A): view of right timbal. (B): view of dorsal surface between tergites 1 and 2 showing the position of the timbals 'sandwiched' between the tergites. Scale bars = 1 mm.

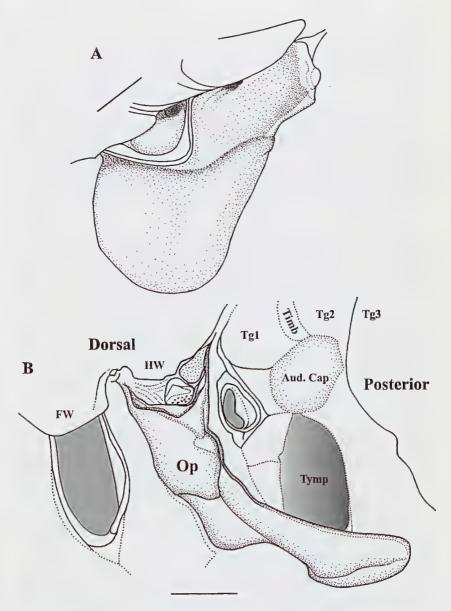


Fig. 6. Froggattoides typicus. (A): ventral surface of left operculum. (B): lateral view of left operculum (Op) and proximal structures. Tymp = tympanum (graded shading); Aud Cap = auditory capsule; FW and HW = bases of fore and hind wings; Tg 1-3 = tergites 1, 2 and 3; Timb = timbal ('sandwiched' between tergites 1 and 2). Two external openings are shown as the shaded areas. Scale bars = 1 mm.

Froggattoides typicus seemingly exhibits certain behavioral and song adaptations to nocturnal activity. First is the constant movement at night within tree foliage, observed as walking in the cages, but is also inferred to include at least short flights in the natural environment (noting their ready attraction to light). This activity starts during dusk, again based on observations on caged specimens. A second aspect is the soft continuing clicking song, here identified as the calling song, emitted during the earlier part of the evening. This song has a dominant frequency range of 6.5–9 kHz, with a weaker extension to about 14 kHz. Additional patterned and single clicks are emitted during this song component, whose frequencies overlap, even slightly extending the range of the continuous calling song. These early evening songs are inferred to be predominantly timbal produced, although some clicks seem to have a wing-flicking component.

The third aspect is the change towards the increasing importance of clicking songs later in the evening, tending to differ in their structures and frequency properties from those emitted earlier. These clicks appear to be produced predominantly through wing flicking, although some have a timbal component. Sound production is again accompanied by movements of the cicadas. These clicks, as described, have very wide frequency ranges, from <2 to ~16 kHz, believed to facilitate sound transmission and localisation. Wing flicking may also be associated with pheromone dispersal, although this remains to be demonstrated. A fourth aspect is the production of the sporadic short, sharp 'buzz' song, which occurs both in the early and especially later evening. The dominant frequency of this component lies between approximately 2 and 10 kHz, thereby effectively complementing the frequency ranges of the other emitted sounds.

A fifth aspect concerns sound interference during nocturnal singing. During the period of the present observations, the only interference encountered was a continuous song of an unidentified cricket. The frequency of this song lies within the narrow range of 4.2-5.1 kHz (Fig. 4A). This is below the dominant frequency of the *F. typicus* calling song and only minimally overlaps with that of the other two song types.

One significant feature of the variety of sounds emitted by *F. typicus* is their resulting broad frequency range. Such frequency ranges are expected to facilitate more efficient survival of song structures which are degraded through absorption, scattering, reflection and refraction, which lead to frequency filtering of sound propagating through foliage (Michelsen 1992, Richards and Wiley 1980, Michelsen and Larsen 1983, Römer and Lewald 1992). The higher frequency components should also aid in sound localisation (Gerhardt and Huber 2002). It is suggested that the early evening calling songs and clicking sounds function to alert and attract females to the presence of males within a given area. The later evening clicking and 'buzz' sounds may facilitate the final stages of localisation of both males and

females. It is likely that females also use wing flicking to respond to male calls (given that female *F. typicus* also possess strongly angulated forewings), as has been observed in a number of diurnal cicada species (Sueur and Aubin 2004).

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